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The Effect of *Rhyssa persuasoria* (L) (Ichneumonidae) on a Population of *Sirex noctilio* F. (Siricidae)

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Abstract

STUDIES of the activity and behaviour of *Rhyssa persuasoria* (L.), a parasite of the larvae of *Sirex noctilio* F., are described. Preliminary tests of the searching ability of the parasite were made and its effect on the numbers of *Sirex noctilio* F. was assessed from four years of sampling infested trees. The work was commenced in March 1957, at Rai Forest, Nelson Province, New Zealand, and completed in 1960.

INTRODUCTION

Rhyssa persuacoria L. was introduced into N.Z. by Miller and Clark in 1928 (Miller and Clark, 1935) in an attempt to control the woodwasp *Sirex noctilio* F. Since that time no assessment of the effect of the parasite on its host had been made. Work done by G. B. Rawlings (personal communication) had indicated that *R. persuasoria* parasitised only one woodwasp larva in every 10 insertions of its ovipositor. Our study was designed to find out what motivated an attack by *R. persuasoria*, whether that attack was always associated with the presence of woodwasp larvae, and, if so, what instar was most attractive or most successfully attacked. The percentage of host larvae present that were found by the parasite in a given time and the ultimate reduction of the siricid population due to parasitism were investigated.

MATERIALS AND METHODS

Logs of *Pinus radiata* D. Don were used in the study of the activity of *Rhyssa persuasoria*. These logs were all about 2 feet long and 2 inches in diameter. Each test was repeated three times with the same mated female of *R. persuasoria* and subsequently repeated with two others.

The logs included some fresh uninfested ones, some in which *Sirex* had recently oviposited, logs containing young larvae, logs containing emergence holes and late-stage larvae and logs from which all woodwasps had emerged. One test was done on wood of *Dacrydium cuppressinum* Soland. containing larvae of the prionid *Prionoplus reticularis* White.

To assess the effect of parasitism of *S. noctilio* by *R. persuasoria* rearings were made from *Sirex*-infested trees of *P. radiata* over a period of four years and totals

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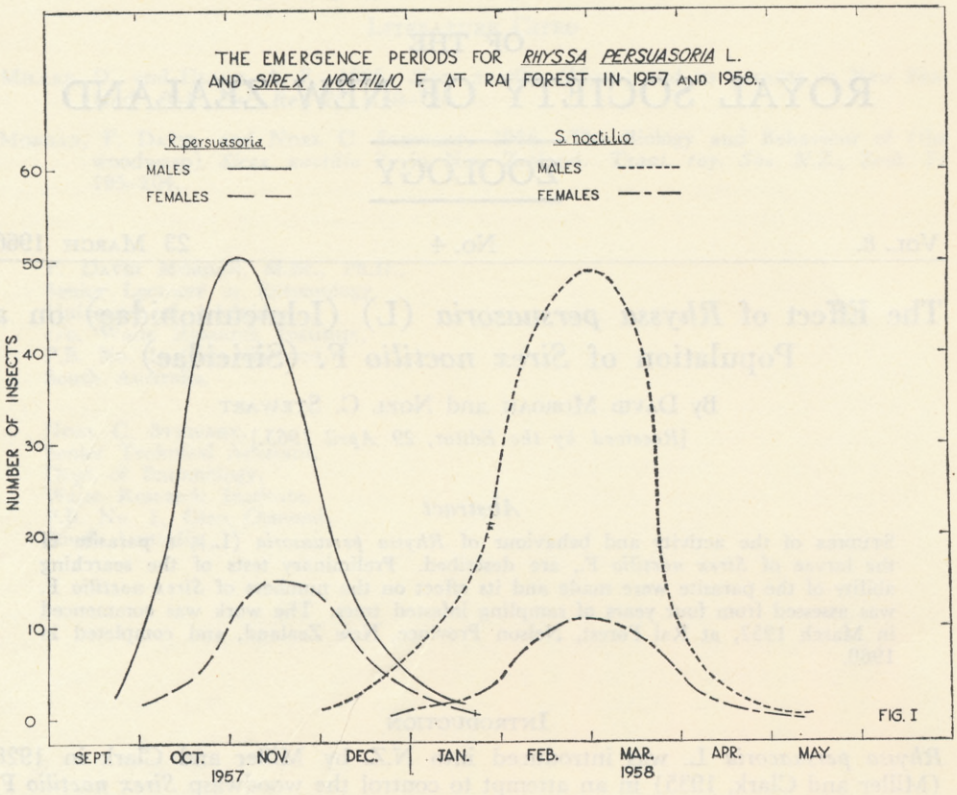

of *R. persuasoria* were compared with totals of *S. noctilio*. Block samples were also taken from other infested trees, opened and larvae removed and counted. Percentage parasitism in each case was determined.

Life History and Behaviour of *Rhyssa persuasoria* (L.)

Adult *Rhyssa persuasoria* begin emerging before those of *S. noctilio* in the early spring, emergence continuing for about four months (Fig. 1). The first males emerge some days before females. Males wait about the probable site of emergence and mate with females as soon as they emerge, the period spent in copulation being from 1.5 to 5 minutes, occasionally longer.

Females appear ready to oviposit about 24–48 hours after mating, when they begin searching the surface of pine logs with the tips of their antennae, tapping along and into crevices and holes in the bark. When about to insert their ovipositor the abdomen is raised almost vertically and the long ovipositor and sheath is brought ventrally, and its tip placed centrally between the front and middle tarsi. During oviposition the ovipositor is guided and supported between the hind coxae, and the sheath bends away to the side ultimately clearing the wood surface and straightening behind the insect before the ovipositor is fully inserted. After removal from the wood the ovipositor is cleaned between the hind tibiae and placed back in its sheath.

The time taken to make one complete insertion and withdrawal varies considerably with the condition of the wood, particularly the presence of siricid oviposition holes and exit tunnels. However, on the average it would take about 15 minutes to complete one oviposition, though times from 3–25 minutes have been recorded.

The presence or absence of a suitable food source was found to be important to the longevity and performance of adult *R. persuasoria.* Tests indicated that unfed adults lived from 5–15 days and oviposited for about 3–8 days of their life. Those fed on watered honey or a sugar paste lived from 12–30 days and oviposited, on the average, for 10–25 days of their life.

R. persuasoria lays its eggs near host larvae, which are apparently stung, because parasitised larvae are almost immobilised when examined just after the egg is laid. The egg hatches in 48–96 hours and the young parasite larva attacks the siricid larva and is fully fed in about 8–12 weeks. The parasite larva then appears to enter a diapause which lasts several months, pupates during the period from late August to November, and emerges over the period September to early January. No pupal cocoon is constructed, pupation is completed within the mine of the host and emergence is achieved by boring directly to the outside from the host tunnel.

ATTRACTION OF *R. persuasoria* TO LOGS INFESTED BY *Sirex noctilio*

Logs, in various stages of infestation by *Sirex noctilio,* were each subjected to attack by a single mated female *R. persuasoria* and a distinct pattern of attraction was found. This is shown in Table I, in which the degree of attraction is shown by the number of + signs per test.

TABLE I

Attraction of Logs of *P. radiata,* infested by *Sirex noctilio,* to *Rhyssa persuasoria* L.
(Tests repeated 9 times with 3 mated females.)

Log No.	Log Condition	*Rhyssa* Activity	
		Searching	Insertion of Ovipositor
1	No infestation	+	
2	Recent oviposition by *S. noctilio*	++	
3	Young *Sirex* larvae present	++	+
4	Exit holes, older *Sirex* larvae present	++++	++++
5	*Sirex* larval tunnels no *Sirex* larvae	++++	++++

Tests were also made with logs of *Dacrydium cupressinum* containing larvae of *Prionoplus reticularis.* While the working of these larvae could be faintly heard, *R. persuasoria* was not attracted. Subsequently, frass from larval tunnels of *Sirex noctilio* was placed in one of the longhorn larval galleries and *R. persuasoria* was immediately attracted to that gallery.

It is apparent from the above that the olfactory sense is involved in the attraction of *R. persuasoria* to its host. This olfactory attraction is not only concerned with the larvae of *Sirex, Rhyssa* being attracted to larval frass and to galleries of *Sirex* in wood containing no larvae. The attraction of wood containing *Sirex* oviposition tunnels and no larvae also supports this statement. It would seem that activity by siricid adults in emerging and in ovipositing is slightly attractive to *Rhyssa persuasoria,* hence the activity around exit holes and oviposition punctures. Strong attraction to larval frass was indicated by the tests, and it could well be that the frass contains some secretion from the larva, or that it contains the symbiotic fungus *Amylostereum chaillettii* (Fr.) Boidin, which could be attractive to the parasite. Wood containing the fungus but without woodwasp larval activity was attractive to *R. persuasoria* but not to the same degree as larval frass.

Tests were then made with *Sirex* larvae, exposed by cutting open an infested log. The parasite was attracted to them but was quick to move away at any

sign of movement from the siricids. Attempts by *Rhyssa* to oviposit through brown paper covering small tubes in which *Sirex* larvae were placed were recorded, but no successful parasitism resulted.

It was therefore concluded that the workings of adult and larval *Sirex noctilio* attracted *Rhyssa persuasoria,* that the attraction was an olfactory one, and that it was due in part to the presence of the symbiotic fungus but mainly to some secretion emanating from both adult and larval *Sirex* and particularly potent in the larval wood-frass.

The Searching Ability of *Rhyssa persuasoria*

Logs containing woodwasp larvae in various stages of development were subjected to attack by mated female *Rhyssa persuasoria* all of about equal size. The oviposition points were marked and these were later cut open and examined.

It was found that the number of successful attacks varied from one in every 5–12 insertions of the ovipositor. The percentage of larvae parasitised varied from less than 1 to 34.

Rarely were larvae younger than the fourth instar parasitised, only one third instar being recorded. Larvae in the fifth and sixth instar, and later larval stages were most frequently parasitised (Table II). (N.B. Log 1B in Table II was exposed to attack in January after oviposition by *Sirex* in late November. All larvae were in the second and third stages. The other logs (2B, 3B, and 4B) were exposed to *Rhyssa* in October after attack by *Sirex* throughout the previous summer and autumn. Instars from IV up to pupae were present.)

Table II

Parasitism of *Sirex noctilio* F. by *Rhyssa persuasoria* (L.) in logs of *P. radiata* subjected to attack in the Laboratory at Nelson, 1957.

Log No.	No. of *Sirex* Larvae Present	Percentage Parasitism	No. of *Sirex* larvae parasitised by Instars					
			II	III	IV	V	VI* Plus	PUPAE
1B	103	0.97		1				
2B	32	34.37			2	4	5	
3B	19	25.38			1	2	2	
4B	51	31.40			1	6	9	
				1	4	12	16	

* N.B.—More than 6 instars may be present in the development of some individuals, and this column probably includes at least a few seventh instars.

See text for details of time of infestation of logs by *Sirex* and subsequent time of selection by *Rhyssa* so that larvae of various instars could be available for parasitism.

Rhyssa persuasoria is apparently not very efficient at finding hosts. It was noted on several occasions that the parasite had barely missed a host larva in one probe but sometimes found another host nearby with one of several other probes. *Rhyssa* may strike a larval tunnel up to an inch away from the host larva and still successfully parasitise the *Sirex*. This depends on the depth of the host in the wood and is apparently accomplished by the ovipositor bending along the *Sirex* tunnel. In most instances, where groups of *Sirex* larvae were within reach of *Rhyssa,* only one or two were parasitised. Such evidence indicates that *Rhyssa persuasoria* is unlikely to exert a strong controlling influence on the numbers of *S. noctilio.*

THE DEGREE OF PARASITISM OF *Sirex noctilio* BY *Rhyssa persuasoria*

Sirex noctilio has a one-year or a two-year cycle of development (Morgan & Stewart, 1966). *Rhyssa persuasoria* is able to parasitise some young *Sirex* larvae only because its emergence period overlaps that of *Sirex* so that some parasites are active when the early instars of the host are developing. The next spring *Rhyssa* is able to attack the entire siricid population in any tree before woodwasp emergence begins. The parasite therefore can attack the woodwasps in three periods over a two-year cycle.

Information on the one- and two-year developmental periods of *Sirex* and the degree of parasitism by *Rhyssa,* was obtained over four years in two ways. The first way was by insectary rearing. In this 10 trees recently killed by *Sirex* and 10 trees from which the first-year emergence had taken place, were felled and placed in insectaries in the spring. By keeping the two types of trees separate and making daily counts and collections of all insects that emerged, re-oviposition in the test trees was prevented and assessments of the numbers of each insect per unit area were possible.

The second method was designed to give more information on the immature stages or earlier information on the population status of both species than obtainable by insectary rearing. The method involved the removal of a piece of the trunk at intervals along the length of each tree. These pieces or blocks were 12 inches long and were removed at ground level, at 4ft 6in (breast height), immediately below the first whorl of living branches, at the 3-inch trunk diameter level, and approximately half way between this and the level of the first green branches. The five blocks from each of 10 trees, in each of the two same categories of the rearing tests, were cut up and all stages removed and counted so that the effect of parasitism by *Rhyssa* could be assessed.

In the insectary rearings, the logs were retained for two years to cover both periods of emergence and then they too were cut up to obtain an assessment of mortality in the immature stages. In the insectary rearings the average number of *Rhyssa* that emerged in each first-year cycle amounted to less than 0.1 per cent of the number of *S. noctilio,* more than 4,700 of the latter emerging each year or an average of more than 470 per tree. Moreover, the parasites that emerged were predominantly males and smaller than average for the species. This would, however, be expected because of the small size of the host larvae available at the time the parent parasites were active the previous summer. The second-year emergence (Fig. 1) showed a different numerical relationship between parasite and host due in part to the greater numbers of suitable host larvae available to the parent parasites when they were active, prior to the main emergence period of their host. The percentage parasitism in the second-year cycle rose to an average 37 per cent over the four years, but this represents the relationship only to the second emergence of *Sirex.* Of the total numbers of insects that emerged per tree over both cycles of development, *Rhyssa* amounted to about 10 per cent per year.

The sample block tests confirmed the above figures. Parasitism varied in degree between trees but the annual average of all tests was remarkably consistent to the above.

We believe that the evidence obtained from these tests (particularly over four years when *noctilio* was at or near the highest numbers it reached for the study areas at Rai Forest) indicates that *persuasoria* exerts a rather small degree of control on its host. It would appear that there is a direct relationship between the evidence on the searching ability of adult *persuasoria* reported earlier and the degree of parasitism recorded. It is unlikely, therefore, that *persuasoria* would have a significant effect on the ability of *noctilio* to increase its numbers when increased resources are available to it.

Discussion

The relationship between *Rhyssa persuasoria* and *Sirex noctilio* merits further investigation. In particular more information on the early stages and the late larval diapause of *Rhyssa* is desirable. Insectary-kept logs tend to lose moisture more rapidly than logs in the field. The former also tend to be in a warmer environment. It is possible that this drier, warmer environment within the wood, inhibits the late larval diapause in at least some individuals of *Rhyssa* which would complete their development in 10–14 weeks instead of 8–10 months. As already stated, *Sirex* is liable to parasitism on three occasions in a two-year cycle. The first of these occurs in the summer of the year that the woodwasp attack is successful and involves those parasites which live into January and February (see Fig. 1). The second is in the following September to January, and the third one year later, or before and during the early part of *Sirex* emergence. Emergences of the parasite have been recorded from the first two attacks but not from the third. Cutting experiments have shown logs, subjected to this third attack, to have some siricid immatures present that appear to be carrying through to a third year. The number of siricids present at this time is low and none has completed development in the period of this study. Any of four reasons may account for the apparent failure of *Rhyssa* to parasitise its host in such logs. First, as hosts are few and the parasite is a poor searcher, there may be little chance of successful parasitism. Secondly, as hosts are few and the general level of parasitism is low, we may not have examined sufficient material to detect the low level of parasitism present. Thirdly, if the late larval diapause is inhibited in the drier logs kept at higher temperatures than in the field, then *Rhyssa*, resulting from the third period of parasitism, may emerge early and be confused with the later emergences resulting from the second. Fourthly, the *Rhyssa* from the third attack may have died because of unsatisfactory conditions in the wood, and if death had occurred in the early stages, the remains may not have been found. Female *Rhyssa* are greatly attracted to logs prior to and during the second emergence of *S. noctilio*. With this degree of activity by a parasite, one would expect some successful parasitism to result. Any of the first three reasons given seems to have merit, but one would tend to give decreased signicance to the fourth because living larvae of *Sirex* can be found in the wood. Certainly, these do not mature, an important factor in this being the rapid progress of *Ceratocystis* sp. and *Diplodia* spp. (fungi apparently lethal to siricid immatures) through infested wood. This progress is assisted by the increased access, for water and fungal spores, that results from the siricid and ichneumonid exists from the logs.

Attempts by *Rhyssa* to parasitise host larvae held in glass tubes covered with brown paper, encourages the belief that successful parasitism might be obtained in this way by varying the technique. In our tests the parasites did not appear to be able to cling well to the surface of the paper. Some surface offering a better foothold to the insects during oviposition, such as bark, might well assist in obtaining parasitism. Should such a technique succeed, the parasitic behaviour of *R. persuasoria* and the development of its immature stages could be examined. If fresh bark is used as the cover over the exposed larvae, it could probably be made attractive for parasitic oviposition by sprinkling it with frass from the tunnels of siricid larvae.

The attraction of *Rhyssa to Sirex* appears to be an olfactory one. In those tests of material rated highly attractive (four + signs; see Table I) the behaviour

pattern was consistent throughout all replicates. As would be expected, the reaction varied in consistency with the drop in attractiveness. For instance in logs in which *Sirex* had recently oviposited two insertions of the ovipositor were recorded in the first test and one in the replicates. The slight attractiveness of wood infested with *Amylostereum chaillettii* might have been due to the presence of a small amount of larval frass, though this was not noticed. It could also have been due to the presence of secretions from siricid larvae, undetected by the visual checks made before the wood specimens were exposed to the parasite. Cultures of the fungus in wood not attacked by *Sirex* could clear up this point.

The significance of adequate food for parasites such as *Rhyssa* is obvious. There is therefore a sound biological reason for the apparently poor performance of this ichneumonid in some pine plantations in New Zealand. There seems little doubt that plentiful sources of nectar within or near the pine stands would result in higher degrees of parasitism, though such may be of local significance only. The inability of the parasite to find a large proportion of available hosts is innate to the insect and therefore unlikely to be something that can be manipulated. Likewise the emergence of *Rhyssa* before the peak emergence of *Sirex* could in itself indicate that the parasite would be less efficient in the control of its host because it could not parasitise more than a small fraction of the potential host larvae in its first attack, since the flight period of the parasite is completed before peak emergence of its host. One might expect a better performance from a parasite that is active after the period of peak emergence of its host because it could have larger numbers of its host to parasitise, thereby giving perhaps an improved chance of parasitism. Perhaps there are species of *Rhyssa* that emerge in the autumn. If so, these should be found and introduced to assist in the control of *S. noctilio*. It is unlikely that *R. persuasoria* could be manipulated so that its emergences would occur naturally 4–5 months later than at present. This could probably be done in warm rooms to speed development, or cold rooms to retard it, but it is probable that once released in the field, it would revert to the former emergence period. It would thus be a case of continuous propagation and annual release which is probably much more expensive in the long term than finding and establishing a species which emerges in the autumn, should such exist.

In this study of the effect of *R. persuasoria* on a population of *S. noctilio* there appears to be evidence that, while the parasite is extremely active, it exerts an insignificant degree of control on the numbers of its host. Though some environmental factors, such as increased food availability, might improve the rate of parasitism, innate characteristics including a life cycle out of phase with that of its host and a lack of ability in the finding of its host, generally tend to reduce the significance of the ichneumonid in the natural control of its host.

It was thought for some years that *R. persuasoria* was not a parasite of *S. noctilio* in Europe but F. Wilson at Silwood Park, England (personal communication) has definitely determined that it is a parasite of *noctilio* in Europe.

Finally, it would appear that aggregations of larvae of *sirex* in the wood may well have significance for the survival of the woodwasp. In these studies *Rhyssa* often left a site where successful parasitism had occurred, despite the fact that several more hosts were available there. It is possible that, once having " worked " a site successfully, *Rhyssa* may make that site unattractive both to itself and to other female parasites which come along later. This could be one way in which hyperparasitism by *Rhyssa* is prevented. Certainly we have not recorded such hyperparasitism and we have noted that female *Rhyssa* do not use the bores made by other females when inserting their ovipositors.

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